ECOLOGY OF UPPER KLAMATH LAKE SHORTNOSE AND LOST RIVER SUCKERS

6. Effects of water quality on growth of juvenile shortnose suckers, *Chasmistes brevirostris* (Catostomidae: Cypriniformes), from Upper Klamath Lake, Oregon.

1999
ANNUAL REPORT (partial)

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March 31, 2000

ABSTRACT

Otolith increment widths are often assumed to be a surrogate for growth. We examined otoliths from 85 juvenile shortnose suckers (Chasmistes brevirostris) caught during their first summer in Upper Klamath Lake in 1997. Water quality, especially un-ionized ammonia, was very poor during 1997. We wanted to determine if sublethal effects, as measured by reduced increment widths, were associated with water quality parameters. Daily growth of individuals was modeled as deviations from a baseline growth curve established from 343 shortnose suckers collected from 1991-1997. We conducted a series of multiple linear regression analyses that considered effects of water temperature, pH, dissolved oxygen, redox potential, conductivity, and un-ionized ammonia concentration. Residuals from this analysis were compared to lake elevation and did not appear to show a significant relationship.

Increment widths were positively significantly correlated with water temperature, and negatively significantly correlated with pH, conductivity, and un-ionized ammonia ($P \leq 0.05$). When un-ionized ammonia was removed from the analysis, temperature was the only significant variable. Within the temperature range experienced by juvenile suckers in 1997, growth was best at higher temperatures. Increment widths closely matched water temperature until mid- to late-summer. Our results indicate that mean increment width and mean water temperature became "uncoupled" when peaks in mean un-ionized ammonia occurred, and that these high un-ionized ammonia levels contributed to declines in mean increment width. We believe that the significant negative effect we see in the full data set is a result of interactions of pH and un-ionized ammonia which are not detected when un-ionized ammonia is removed from the analysis. This analysis indicates that juvenile shortnose suckers that survived poor water quality in 1997 had a measurable sublethal reduction in growth, manifested as a significant decrease in otolith increment widths.

INTRODUCTION

The shortnose sucker, *Chasmistes brevirostris* (Cope 1879), and Lost River sucker, *Deltistes luxatus* (Cope 1879) are endemic to the Upper Klamath Basin of southern Oregon and northern California. Upper Klamath Lake in south central Oregon is primary refuge for the two species (Buettner and Scoppettone, 1990). Although historically abundant, these species were listed as endangered (USFWS, 1988) in 1988 based on studies documenting that populations were declining in size and aging due to apparent recruitment failure since the early 1970s. Hypotheses linking ongoing recruitment failure to fishing pressure, water-development projects, pollution, habitat reduction, hybridization, and the introduction of exotic species have been proposed by several authors (Andreasen, 1975; Buettner and Scoppettone, 1990; Scoppettone and Vinyard, 1991; USFWS, 1993; Martin and Saiki, 1999).

Growth and mortality during the early life history stages of fishes are important components in understanding recruitment dynamics of populations. Tenfold or greater fluctuations in recruitment can be precipitated by a relatively small variation in mortality or growth rates (Houde, 1987). By understanding the processes that affect mortality and growth rates of larval and juvenile fishes, researchers may be able to determine both biological and environmental factors that impact recruitment variability.

Use of otolith data in fisheries research accelerated after Pannella (1971) first described daily otolith growth increments in some cold-temperate fishes. The deposition of daily and annual increments in fish otoliths has been validated by a number of researchers for several species (see review by Secor et al., 1991), including both shortnose and Lost River suckers (Hoff et al., 1997). In addition to obtaining key information such as population age structure and hatchdate distributions from increment counts, otoliths may also allow estimates of individual growth through the examination of increment widths (Gutiérrez and Morales-Nin, 1986; Eckmann and Rey, 1987; Karakiri and von Westernhagen, 1989; Molony and Choat, 1990; Williams and Lowe, 1997). The use of otolith width data can be extremely valuable to the researcher if a positive relationship

can be established between increment width and somatic growth (Secor and Dean, 1989). During stressful conditions, otolith growth and somatic growth can become uncoupled, with somatic growth slowing or stopping while metabolic-dependent otolith growth may continue or increase (Neilsen and Geen, 1985; Gutiérrez and Morales-Nin, 1986; Molony and Choat, 1990; Simon et al., 1996). Preliminary analyses by Simon et al. (1996) indicated that, under non-lethal conditions, otolith and somatic growth are coupled in shortnose and Lost River suckers.

Poor water quality and the hypereutrophication of Upper Klamath Lake may act as a stressor to suckers and impact recruitment. During summer, massive blooms of the blue-green algae, *Aphanizomenon flos-aquae,* occur in Upper Klamath Lake and contribute to large-scale diurnal fluctuations in water quality parameters such as dissolved oxygen and pH (Phinney et al., 1959, Bortleson and Fretwell, 1993). Post-bloom decay of phytoplankton and other organics contribute to lakewide toxic levels of un-ionized ammonia and low levels of dissolved oxygen; this is especially true along the western shore of the lake, where wind drift and currents concentrate large algal populations (Phinney et al., 1959; Bortleson and Fretwell, 1993; Martin and Saiki, 1999). Stressful conditions caused by poor water quality have been implicated in fish kills in Upper Klamath Lake during summer 1996 (Perkins et al., 1996).

Extremely high levels of un-ionized ammonia were recorded in several regions of Upper Klamath Lake in 1997, especially along Eagle Ridge and in Howard Bay (J. Kann, Aquatic Ecosystem Sciences, unpubl. data). Un-ionized ammonia is toxic to fishes at relatively low concentrations (Tucker et al., 1984; Rasmussen and Korsgaard, 1996; Saiki et al., 1999), and in 1997, un-ionized ammonia concentrations in Upper Klamath Lake reached levels toxic to suckers (Saiki et al., 1999). During long-term surveys of suckers in Upper Klamath Lake (Simon et al., 1998), we collected juvenile suckers during and after this high ammonia event.

The purpose of this study was to examine the relationship between daily otolith increment widths in juvenile shortnose suckers and daily water quality

parameters during their first summer of growth in Upper Klamath Lake in 1997. We were specifically interested in whether sublethal effects of high un-ionized ammonia could be detected in the form of reduced daily increment widths. Small numbers of Lost River suckers during the sampling period precluded their use in the analyses.

METHODS

Juvenile suckers

Baseline data for suckers was collected from our long-term surveys of juvenile suckers in Upper Klamath Lake from 1991 and 1993-1996. The water quality analysis was based on juvenile suckers collected at three-week intervals from June through October, 1997 using two gear types: a 6.1-m beach seine with a 2x2x2-m bag and 4.8-mm bar mesh, or a 5-m diameter multi-filament cast net with 6.3-mm bar mesh. The 1997 survey employed both fixed-site beach seine sampling from mid-June through mid-August and a random-stratified cast net survey from late August through early October.   Suckers were preserved and stored in 95% ethanol. Details of sampling design were provided in Simon et al. (1998).

Otolith preparation

All suckers brought back to the laboratory were identified to species and measured for standard length to the nearest 0.01-mm. Right lapilli were removed using a dissecting microscope and fine probes. Otoliths were cleaned in 10% bleach for 30 minutes, rinsed twice with deionized water, and given a final rinse of 95% ethanol to remove any residual moisture. Otoliths were placed in uncapped screw top scintillation vials and allowed to air dry for several days in a clean, dry environment. Once dry, the otoliths were weighed to the nearest 0.0001-mg using a Cahn 29 Electrobalance.

Each lapillus was mounted distal side up on a petrographic slide with Crystalbond thermoplastic resin. Otoliths were then ground by hand along the sagittal plane using 1500-grit wet/dry sandpaper to gain proximity to the core,

and polished using a synthetic velvet cloth and 0.05 μm alumina powder. It was necessary to flip the otolith several times during grinding and polishing in order to create a thin section with visible increments along the entire diameter of the otolith.

Hoff et al. (1997) previously validated daily lapillus increments for these species using known-age hatchery-raised larvae and alizarin complexone-marked wild-caught larvae and juveniles. For this study, daily increments were counted and measured to the nearest 0.0001 μm using a digital imaging system equipped with Optimas 5.0 (1995) software. A counting transect from core to edge along the leading growth axis was consistently used for counting and measuring otolith increments. All counts and measurements were made without information regarding fish length or catch date. Our analyses were based on seven-day moving averages of increment width data.

Water quality

Daily water quality data (temperature, dissolved oxygen, pH, conductivity, and redox potential) were obtained from four open water sites in Upper Klamath Lake at hourly intervals from early May through early October, 1997 (M. Berg, U.S. Bureau of Reclamation, unpubl. data) (Figure 1). Surface un-ionized ammonia concentrations were taken at two-week intervals from eight open water sites from late January through late September (J. Kann, Aquatic Ecosystem Sciences, unpubl. data) (Figure 1). Daily water quality data were reduced by calculating lakewide mean values for our analyses. Because pH values are log based, means were obtained by converting pH values to hydrogen ion concentrations, averaging those concentrations, and then converting back to pH values. Mean daily values for water temperature, pH, conductivity, and redox potential were taken from observations made when those values would be highest, 1100-1500 hrs, while dissolved oxygen values were taken from observations when its value would be lowest, 0400-0800 hrs.

We used seven-day moving averages for all water quality data. This had the greatest impact on the bi-monthly un-ionized ammonia data and resulted in

the same un-ionized ammonia reading being applied to the three days before and after the day of collection. For all other water quality parameters the smoothing of data helped fill data gaps caused by periodic failure of water quality probes in the field.

Modeling the baseline growth curve

Our analysis strategy was to estimate a "baseline" growth curve--i.e., a trajectory of increment width vs. age that we expect would be followed by fish growing in identical, unchanging environments--and then relate departures from that baseline to the environmental variables. In the absence of empirical information on the form of such a curve, we experimented with a variety of possible baselines, including:

1. A constant, age-independent increment width for each fish, estimated as the mean width of that fish's increment measurements;
2. A trajectory for each fish that is parallel to a plot of mean increment width vs. age obtained by aggregating data from juveniles of that species collected in 1991 and 1993--1997 (Figure 2 showing nonparametric smoothed fits for 343 shortnose and 230 Lost River suckers. The increased vertical scatter for older fish is due to the smaller number of specimens contributing data for those ages.); and
3. A trajectory obtained by applying a nonparametric scatterplot smoother available in the S-PLUS language (Cleveland, 1979; MathSoft, 1996) to each fish's width-vs.-age data.

Figure 3 shows examples of the three baseline curves fit to the data from an individual shortnose sucker. For each fish, baseline 1 was obtained by simply averaging the increment widths for that fish, and baseline 3 is a nonparametric smoothed fit to that fish's trajectory of increment width vs. age (from the S-PLUS function lowess).

In the absence of empirical information on the "true" form of the baseline growth curve, the choice of which one to use in our analyses was problematic. The age independence of baseline 1 seemed biologically unreasonable. It tended to create runs of negative and positive residuals that might be interpreted as environmental effects, when in fact it is quite plausible that they represented ontogenetic changes in the growth rate of the otolith. On the other extreme, the fish-specific, nonparametric smoothed curves (baseline 3) seemed too closely tied to individuals' growth trajectories, and they may be "adjusting out" important environmental influences on growth rate. After much exploration of the consequences of using these different baselines, we chose to adopt baseline 2 as a "best guess" compromise between the extremes represented by the other two baselines. Even though the horizontal axes in Figure 2 represent age, not calendar date, there is a general tendency for points on the left to come from earlier in the season than points on the right. Consequently, there remains a real potential for confounding of ontogenetic and environmental influences on growth rate.

Statistical analyses

Our general model for the increment width of fish i at age t_j (in days) is:

$$y_{ij} = f(t_j) + \eta_i + x_j\beta + \varepsilon_{ij},\qquad(1)$$

where $f(\cdot)$ is the possibly nonlinear function of time that we have chosen as our baseline growth curve; η_i is a random effect due to fish i, x_j is a row vector of the environmental variables recorded on the date that this fish was age j; β is a vector of regression parameters; and $\varepsilon_{i1}, \varepsilon_{i2},\ldots,\varepsilon_{in_i}$ are sequential errors for fish i, assumed to represent a first-order autoregressive process, abbreviated AR(1). That is, increment width is the sum of a baseline value, a random effect due to the individual fish, "effects" of the environmental variables, and a random error. The AR(1) structure implies that the correlation of the errors from an individual fish on days i and j is $r^{|i-j|}$, where r is the autoregression coefficient ($-1 < r < 1$).

Our strategy was to estimate the baseline, subtract it from the observed increment width, and then model the difference as

$$z_{ij} \equiv y_{ij} - f(t_j) = \eta_i + x_j\beta + \varepsilon_{ij}. \qquad (2)$$

This is a linear mixed-effects model (Laird and Ware, 1982; Diggle et al., 1994) with serial autocorrelation of the random errors within fish. We fit the model using the S-PLUS function lme, choosing restricted maximum likelihood as the method of parameter estimation (Venables and Ripley, 1997).

Models were run with the full water quality data set and with un-ionized ammonia removed from the data set. Residuals obtained from the reduced data model were plotted against un-ionized ammonia concentration and residuals from the full data model were plotted against lake level to further explore relationships with increment width.

We also explored a method of inference based on individual estimates, as discussed by Davidian and Giltinan (1995). For each fish, we regressed increment width residuals against environmental predictors, adjusting for first-order serial correlation. Results for the entire sample of n fish were summarized as sets of n regression coefficients for each predictor, and statistical inference was based on these independent estimates. The computations in our implementation of this approach were more time-consuming than those for the "pooled" approach described above, and the resulting variance estimates tended to be larger, so we have chosen to emphasize the first method here.

RESULTS

Mean increment width and water quality variables over time

We plotted mean increment width vs. each water quality variable to graphically compare variations in increment width with fluctuations in water quality (Figures 4-9). Mean increment width tended to increase steadily through time (from Julian day 124 to 204) before beginning a decreasing trend after Julian day 204. Increased scatter in the mean increment width after Julian day 240 reflects relatively few fish contributing data for those days. Mean water temperature (Figure 4) exhibited a similar trend with minor fluctuations, with

values steadily increasing over time until peaking on day 218 (23.14° C), and decreasing thereafter. Minor fluctuations in the water temperature signal matched increment width data well. Mean increment width generally increased and decreased in parallel with mean water temperature up to Julian day 212 (Figure 4). After this date, mean increment width remained depressed even though mean water temperature increased and eventually peaked on Julian day 218 before steadily decreasing over the remainder of the season. Mean water temperatures never approached the mean 96-hour median lethal concentration (LC_{50}) reported for juvenile shortnose suckers (30.35°C, Saiki et al., 1999).

Mean un-ionized ammonia concentrations (Figure 5) remained relatively low from Julian day 127 through Julian day 168 (0.0020 to 0.2570 mg/L). Mean concentration peaked to 1.1020 mg/L on Julian day 184, dropped slightly to 0.8454 mg/L on day 202, peaked again to 1.4631 mg/L on Julian day 212, and then decreased again to relatively low levels throughout the rest of the year. These spikes in mean un-ionized ammonia concentrations were 1.6 to 2.7 times the mean 96-hour LC_{50} value reported for shortnose suckers (0.53 mg/L, Saiki et al., 1999). The decrease in mean increment width after Julian day 204 coincided with the timing of the second spike of mean un-ionized ammonia concentration.

Mean pH (Figure 6) exhibited a rapid increase early in the season before leveling out at approximately 9.3 from Julian day 153 to 186. Days 186 through 216 were characterized by relatively large fluctuations in mean pH values over short time periods (changes from 0.5 to 1.19 units in one day). pH fluctuated from a high of 8.91 to a low of 7.09 over the remainder of the season. Although the rapid fluctuations occurred at approximately the same time as the rapid decrease in mean increment width, mean pH values never exceeded the mean 96-hour LC_{50} value reported for juvenile shortnose suckers (10.39, Saiki et al., 1999).

Mean conductivity (Figure 7) appeared relatively stable through time, while both mean dissolved oxygen concentration (Figure 8) and mean redox potential (Figure 9) were cyclical through time. These parameters did not appear to be strongly tied to mean increment width. Mean dissolved oxygen concentrations

ranged from a high of 10.53 mg/L on Julian day 159 to a low of 3.91 mg/L on day 232, but never approached the mean 96-hour LC_{50} value for juvenile shortnose suckers (1.34 mg/L, Saiki et al., 1999).

Effects of water quality variables on mean increment width

Tables 1-4 show the results of applying the linear mixed-effects model (Equation 2) to the residuals from baseline 2. In Table 1, seven-day moving averages of all six water quality variables were included in the fits, and dissolved oxygen and redox potential proved to be the only predictors with no significant association with the response (P = 0.3614 and 0.1006, respectively). Table 2 shows results of backwards stepwise variable selection, where we eliminated non-significant dissolved oxygen and redox potential from the model. Water temperature was positively correlated with increment width, while pH, conductivity, and un-ionized ammonia were negatively correlated. The relatively large-magnitude regression coefficients for temperature (0.1090) and un-ionized ammonia (-0.1308) were an order of magnitude larger than the regression coefficients for pH and conductivity (-0.0690 and -0.0246, respectively). In order to determine if decreasing lake level contributed to decreased growth in shortnose suckers, we plotted the residuals obtained from this model against lake level (Figure 10) and saw no obvious trends.

To examine the robustness of the effect of un-ionized ammonia on increment width, we re-analyzed the data by excluding un-ionized ammonia from the model (Table 3). The only non-significant predictors were pH and dissolved oxygen (P = 0.3735 and 0.0831, respectively). After performing backwards stepwise variable selection (Table 4), redox potential and conductivity also became non-significant (P = 0.0890 and 0.0725, respectively), leaving water temperature as the only significant predictor (P = 0.0000). We plotted the residuals from this model against un-ionized ammonia concentration (Figure 11) and saw no relationship.

DISCUSSION

Mean daily otolith increment widths clearly mirrored mean daily water temperature (Figure 4). Water temperature was also the only water quality parameter that was significant in all regression analyses and the only parameter that was significantly positively associated with increment width (Tables 1-4). Within the temperature range experienced by juvenile suckers in 1997, growth was best at higher temperatures.

Several studies have documented a positive relationship between water temperature and fish growth at optimal temperatures in that otolith growth is influenced by temperature through the effect of temperature on metabolic rate (Townsend and Graham, 1981; Gutiérrez and Morales-Nin, 1986; Karakiri and Westernhagen, 1989; Bradford and Geen, 1992). Mean water temperature in Upper Klamath Lake barely exceeded 23° C., well below the critical mean thermal maximum of 32.7° C. reported by Castleberry and Cech, Jr. (1993) and the mean 96-hour LC_{50} value for juvenile shortnose suckers of 30.35° C. reported by Saiki et al. (1999). These results suggest that water temperatures in Upper Klamath Lake in 1997 were not a source of stress for juvenile shortnose suckers. Even if shortnose suckers experienced pockets of high water temperature (found especially in surface algal scums) (Bortleson and Fretwell, 1993), they could seek cooler water temperatures near the bottom or around cold-water springs and riverine inputs (Buettner and Scoppettone, 1990).

Mean daily otolith increment widths were less clearly related to other water quality parameters (Figures 5-9). The linear mixed-effects model with the full data set indicated that increment widths were not related to redox potential or dissolved oxygen (Tables 1 and 2). This model indicated that pH, conductivity and un-ionized ammonia were all significantly negatively related to increment widths with un-ionized ammonia having the largest effect. Residuals from the full data set model had no clear relationship with lake elevation and all but one were not significantly different from zero (Figure 10). The tendency for growth to be positive when lake elevation was lowest (below 4140.6 ft) may mean that growth

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was better relative to our baseline years that included low, late season lake levels during the 1990's drought years. Samples sizes were also very small later in the season when lake elevations were low and variance was high (Figure 10), thus the trend is not significant. However, the trend might reflect a real biological process if fish that survived the 1997 summer events had greatly reduced competition later in the season when lake levels were low and, therefore, experienced better growth than normal.

The un-ionized ammonia data were collected every two weeks and our analyses applied each of these point observations to a seven-day period adjacent to the date of collection. Despite the shortcomings of the data set, especially the loss of increment comparisons for intervening days, we believe this analysis is consistent with an interpretation that high un-ionized ammonia concentrations had a negative sublethal influence on otolith increment widths and presumably juvenile growth in shortnose suckers. We interpret the results of the full data set model (Tables 1 and 2) as indicating that high pH, conductivity and un-ionized ammonia levels had a significant negative sublethal effect. Removal of ammonia from the model reduces (Table 3) or eliminates (Table 4) significant effects of these other variables. Our analyses removed autocorrelation effects but did not account for cross correlations or interactions. It is well established that toxic un-ionized ammonia comprises a higher percentage of the total ammonia at higher pH and temperature (Colt and Tchobanoglous, 1978; Haywood et al., 1980; Bortleson and Fretwell, 1996; Rasmussen and Korsgaard, 1996). Thus we believe that the significant negative effect we see in the full data set is a result of interactions of pH and un-ionized ammonia. We also believe that inspection of the gross patterns in mean increment width and temperature (Figure 4) was also consistent with this interpretation. Increment widths followed the rise and fall of water temperature until un-ionized ammonia spiked up to high concentrations. Mean increment widths declined at this point, even though temperatures eventually peaked one week later.

Un-ionized ammonia is toxic to fish at relatively low concentrations (Ball, 1967). At sublethal levels, un-ionized ammonia may reduce growth by several

mechanisms, including reduction of oxygen uptake ability due to damaged gill tissue, increased loss of ions due to increased urine flow, inhibition of sodium uptake, decreased food assimilation, and increased susceptibility to parasite epizootics (Colt and Tchobanoglous, 1978; Soderberg et al., 1983; Rasmussen and Korsgaard, 1996). Our results indicate that mean increment width and mean water temperature became "uncoupled" when peaks in mean un-ionized ammonia occurred, and that these high un-ionized ammonia levels contributed to declines in mean increment width. Mean un-ionized ammonia concentration in Upper Klamath Lake exceeded the mean 96-hour LC_{50} value (for juvenile shortnose suckers) of 0.53 mg/L reported by Saiki et al. (1999) for almost a month in late June and late July and peaked at a value three times the 96-hour LC_{50} value on Julian day 212. Martin and Saiki (1999) noted no lethal effects of un-ionized ammonia on Lost River suckers in Upper Klamath Lake in 1995, when concentrations reached 0.78 mg/L; however, the 96-hour LC_{50} value for Lost River suckers is 0.25 mg/L higher than that of shortnose suckers, and they did not investigate sublethal effects on growth. It was interesting to note that we found no dead or moribund suckers during our sampling survey in 1997, indicating that refugia with relatively good water quality may exist in Upper Klamath Lake.

Intense photosynthetic activity and senescence of blooms of *Aphanizomeneon flos-aquae* during late spring through early fall contribute to fluctuations in pH on a daily basis, with maximum values typically reached in the afternoon when photosynthetic activity is highest. In past years, summertime pH values exceeding 10 have been documented for Upper Klamath Lake (Wood et al., 1996; Kann and Smith, 1999). Saiki et al. (1999) reported that at high pH levels, sucker larvae and juveniles experienced convulsions, erratic swimming, and excessive mucous production, and determined a mean 96-hour LC_{50} value for juvenile shortnose suckers of 10.39. During the course of this study, high mean pH values measured during June and early July approached the above-mentioned LC_{50} value, but never exceeded it. Results from other studies (Martin and Saiki, 1999; Saiki et al., 1999) indicate no lethal effects of high pH on larval

and juvenile suckers and suggest that high pH may not be sustained long enough in Upper Klamath Lake to directly cause mortality. Results from this study indicated that sucker growth continued to increase despite times when mean pH values were highest, indicating that other water quality parameters (such as increasing temperature) may play a more important role in regulating growth.

Even though the effect of dissolved oxygen concentration on growth proved non-significant in both our linear mixed-effects models, several studies have documented deleterious effects of low dissolved oxygen on fish physiology (Castleberry and Cech, Jr., 1993; Martin and Saiki, 1999; Saiki et al., 1999). For our study, mean dissolved oxygen proved non-significant simply because the cyclical nature of the dissolved oxygen signal did not match well with the rise and fall of mean increment width. Hypoxic conditions have been shown to exist in Upper Klamath Lake (Wood et al., 1996; Martin and Saiki, 1999); site-specific dissolved oxygen concentration often drops below the mean 96-hour LC_{50} value for shortnose suckers of 1.34 mg/L (Saiki et al., 1999). The lowest mean dissolved oxygen concentration measured in 1997 was 3.91 mg/L. On a smaller scale, low dissolved oxygen levels may stress suckers and reduce their tolerance to high levels of pH and un-ionized ammonia. Conversely, high dissolved oxygen levels may allow suckers to better tolerate deleterious levels of other water quality parameters (Serafy and Harrell, 1993).

Another factor which may affect sucker growth and mortality are algal toxins produced by senescing *Aphanizomenon flos-aquae* and *Microcystis aeruginosa* (Bortleson and Fretwell, 1993; English et al., 1993; Wood et al., 1996). These alkaloid toxins block sodium channels in nerves and paralyze skeletal and respiratory muscles, causing mortality from respiratory arrest (Gorman and Carmichael, 1988; English et al., 1993). Although these toxic algal strains have yet to be reported as occurring in Upper Klamath Lake (Saiki et al., 1999), and their detection is beyond the scope of this study, the presence of these toxins and their possible effects on fish health should not be discounted.

The use of Upper Klamath Lake water for irrigational purposes, release of

water for downstream endangered salmonids, and natural evaporation result in decreasing lake levels over a time period of several months. It has been proposed that an increased frequency of sediment resuspension at low lake levels (due to increased bottom shear stresses) could contribute to increased phosphorus loading (Jacoby et al., 1982) and increased algal sediment recruitment (Wood et al., 1996), which could lead to more intense algal blooms and greater variations in pH, dissolved oxygen, and un-ionized ammonia concentrations. Although previous studies (Wood et al., 1996) have shown a connection between algal growth, pH, and dissolved oxygen, and have linked increased algal populations with decreased lake elevations, the plot of growth residuals vs. lake level indicated no significant change in growth with decreasing lake levels (Figure 10). Lake level was not included in the linear mixed-effects models because of a strong potential for confounding of lake level with other factors that vary smoothly over time (such as water temperature).   The absence of a relation between growth and lake level indicates that, at least for 1997, the drop in lake level was not sufficient to cause a change in growth. Unknown factors, such as larger drops in lake level over time or lower lake levels earlier in the season may (or may not) affect fish growth.

Further refinements to this analysis are needed. The analyses did not explore possible interactions among environmental variables or time lags between the onset of stress and physiological effects in fish. For example, Molony and Choat (1990) reported a 15-day time lag between starvation and reduced daily increment widths in glass fish, *Ambassis vachelli,* and Lehodey and Grandperrin (1996) report a time lag of several months between temperature fluctuations and annular increment widths in alfonsino, *Beryx splendens.* Because un-ionized ammonia concentration was measured only once every two weeks, we have no idea how the concentrations varied between sampling periods. In a related study, Martin and Saiki (1999) reported that water temperatures and unionized ammonia levels in Upper Klamath Lake in 1996 were not directly responsible for instances of high fish mortality in caged suckers. However, unionized ammonia levels never reached median tolerance limits for

suckers during that study period. Further, the study did not investigate any sub-lethal effects of unionized ammonia on fish health. Further controlled investigations into the effects environmental extremes have on sucker growth and mortality would lend insight on those factors, both biological and environmental, that play important roles in fish survival and recruitment.

Several laboratory studies have attempted to relate reduced growth and/or increased mortality in fishes to extremes in water quality parameters (temperature - Ré, 1983; Gutiérrez and Morales-Nin, 1986; Karakiri and von Westernhagen, 1989; Bradford and Geen, 1992; Bestgen and Bundy, 1998; pH - Geen et al., 1984; un-ionized ammonia - Ball, 1967; Colt and Tchobanoglous, 1978; Haywood et al., 1980; Rasmussen and Korsgaard, 1996; dissolved oxygen - Haywood et al., 1980; Baltz, et al., 1995). Several recent studies have examined laboratory tolerances of shortnose and other suckers to a suite of environmental parameters (Castleberry and Cech, Jr., 1993; Bellerud and Saiki, 1995; Kann and Smith, 1999; Martin and Saiki, 1999; Saiki et al., 1999). The present study is unique in that we were able to examine sublethal effects of water quality on sucker growth in a natural environment during a period characterized by lethal concentrations of un-ionized ammonia.

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Table 1. Regression coefficients, standard errors, and *P*-values from the linear mixed-effects full data set model applied to baseline 2 increment width residuals. Entries in boldface are statistically significant (*P*<0.05).

Variable	Regression coefficient	Std. error	*P*
water temperature	**0.0868**	0.0221	0.0000
pH	**-0.0697**	0.0222	0.0017
conductivity	**-0.0266**	0.0035	0.0000
redox potential	-0.0003	0.0002	0.1006
dissolved oxygen	-0.0153	0.0168	0.3614
un-ionized ammonia	**-0.1478**	0.0298	0.0000

Table 2. Regression coefficients and standard errors from the linear mixed-effects full data set model applied to baseline 2 increment width residuals, with backwards stepwise variable selection. Entries in boldface are statistically significant (*P*<0.05).

Variable	Regression coefficient	Std. error	*P*
water temperature	**0.1090**	0.0160	0.0000
pH	**-0.0690**	0.0220	0.0017
conductivity	**-0.0246**	0.0033	0.0000
redox potential	-	-	-
dissolved oxygen	-	-	-
un-ionized ammonia	**-0.1308**	0.0277	0.0000

Table 3. Regression coefficients, standard errors, and *P*-values from the linear mixed-effects reduced data set model applied to baseline 2 increment width residuals. Entries in boldface are statistically significant (*P*<0.05).

Variable	Regression coefficient	Std. error	*P*
water temperature	**0.0792**	0.0110	0.0000
pH	-0.0094	0.0106	0.3735
conductivity	**-0.0046**	0.0022	0.0411
redox potential	**-0.0002**	0.0001	0.0442
dissolved oxygen	0.0140	0.0081	0.0831

Table 4. Regression coefficients and standard errors from the linear mixed-effects reduced data set model applied to baseline 2 increment width residuals, with backwards stepwise variable selection. Entries in boldface are statistically significant ($P<0.05$).

Variable	Regression coefficient	Std. error	P
water temperature	**0.0831**	0.0101	0.0000
pH	-	-	-
conductivity	-	-	-
redox potential	-	-	-
dissolved oxygen	-	-	-
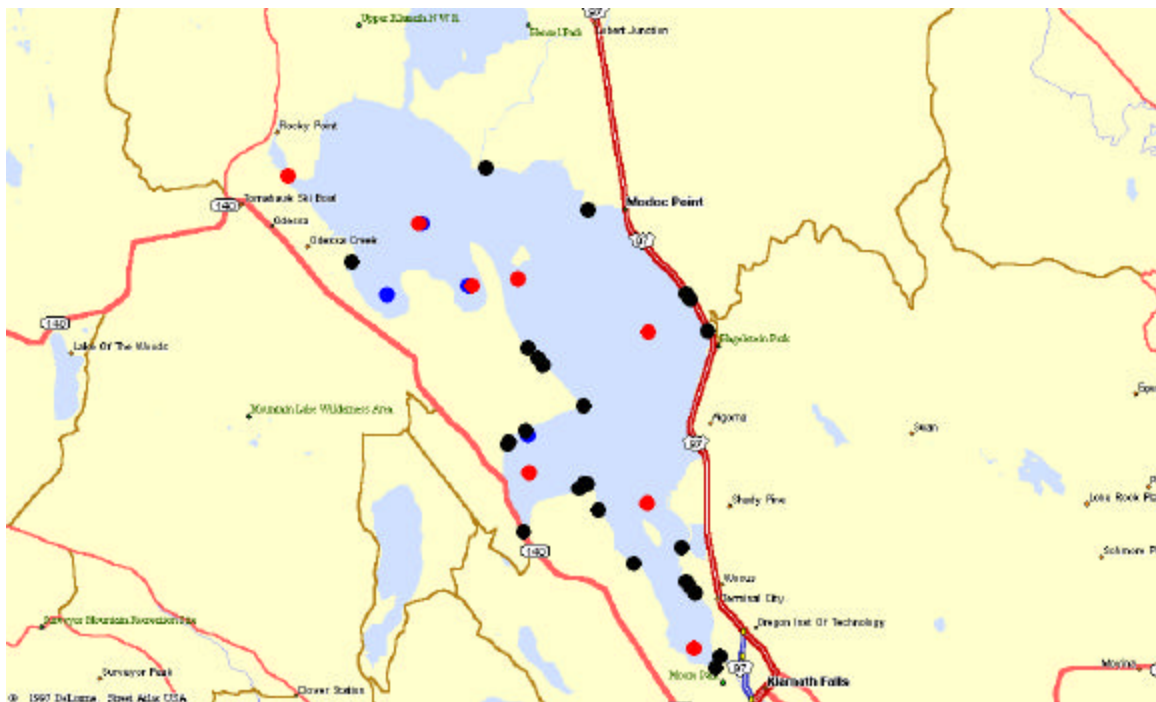
Figure 1. Map of Upper Klamath Lake, Oregon. Black circles represent sites where shortnose suckers were caught; blue circles represent sites where daily water quality parameters (water temperature, pH, conductivity, dissolved oxygen, and redox potential) were measured; red circles indicate sites where un-ionized ammonia concentrations were measured.
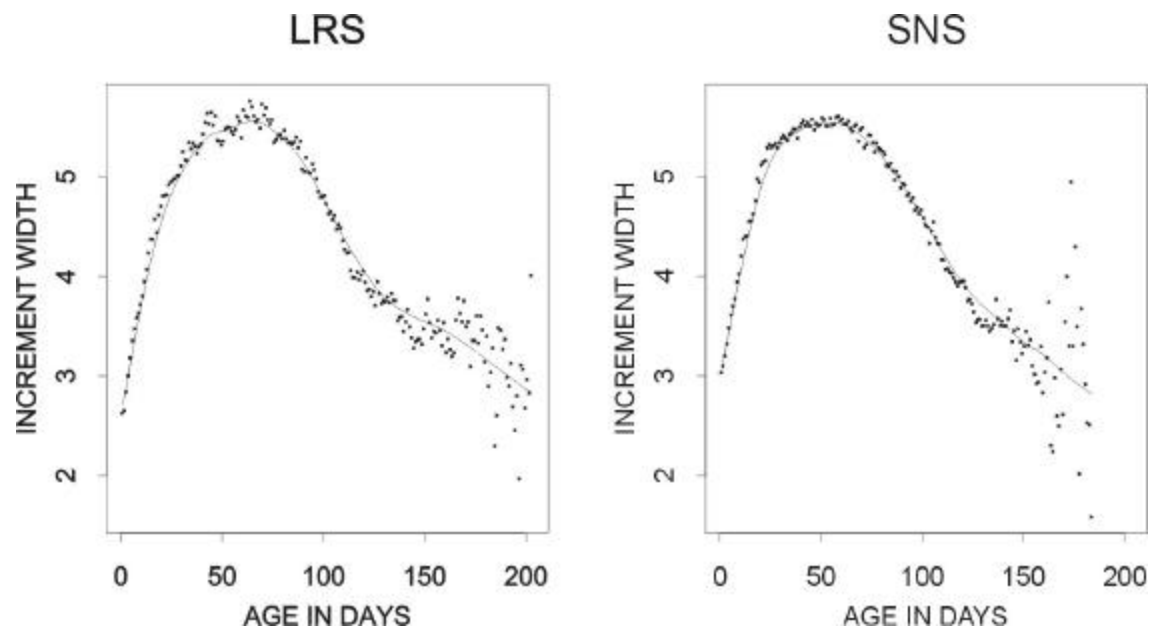
Figure 2. Mean increment widths (: m), over years 1991, 1993-1997, vs. age (days) for juvenile Lost River (LRS) and shortnose (SNS) suckers. Fitted curves were obtained from the S-PLUS function supsmu.
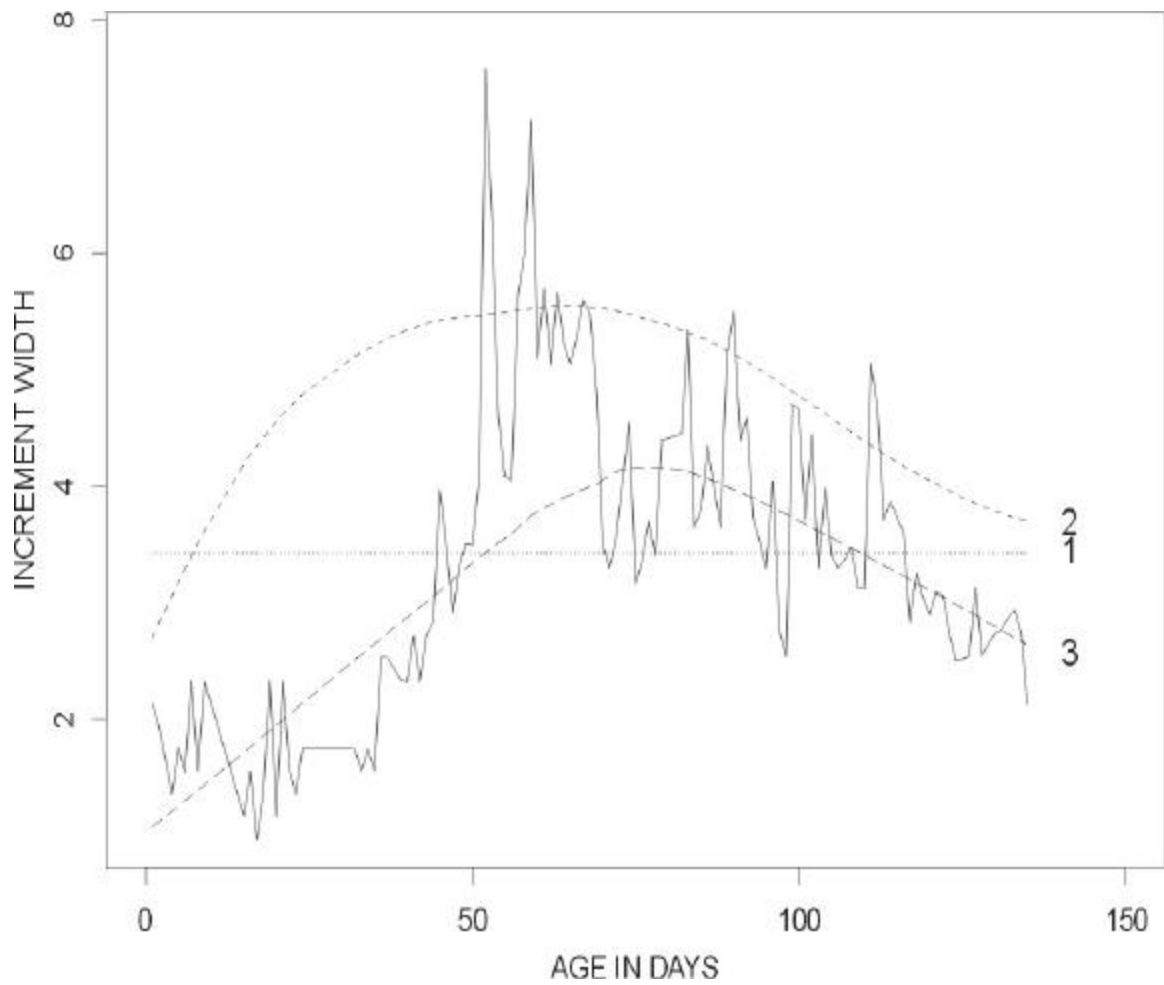
Figure 3. Mean increment width (μm) vs. age (days) for an individual shortnose sucker, with three baseline curves superimposed. The random effect for fish in Equation 2 allows baseline 2 to be shifted up or down for individual fish.
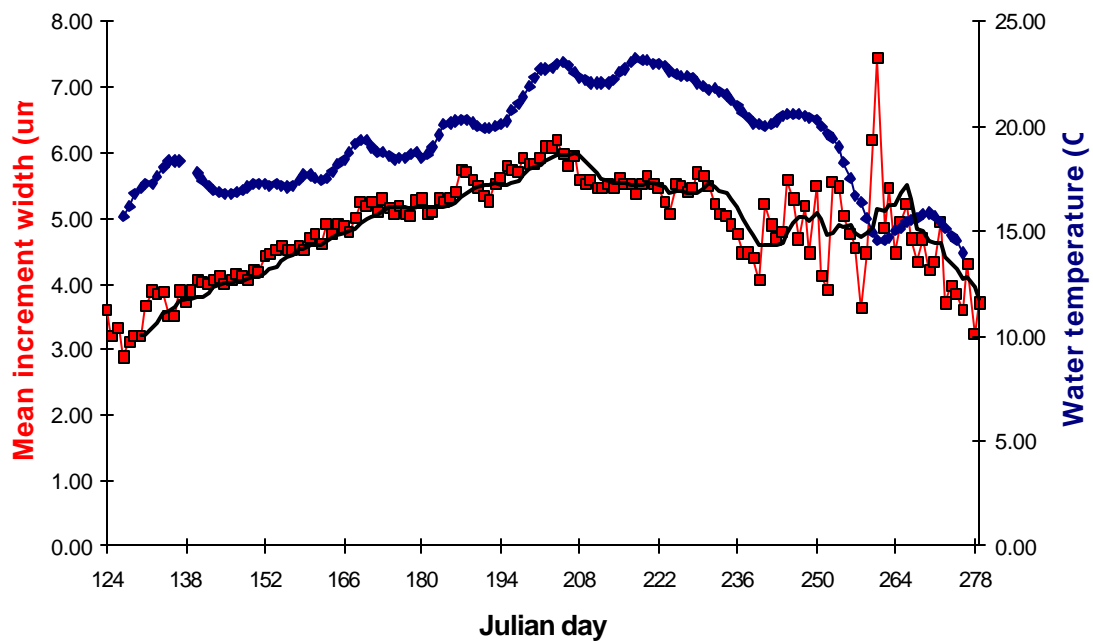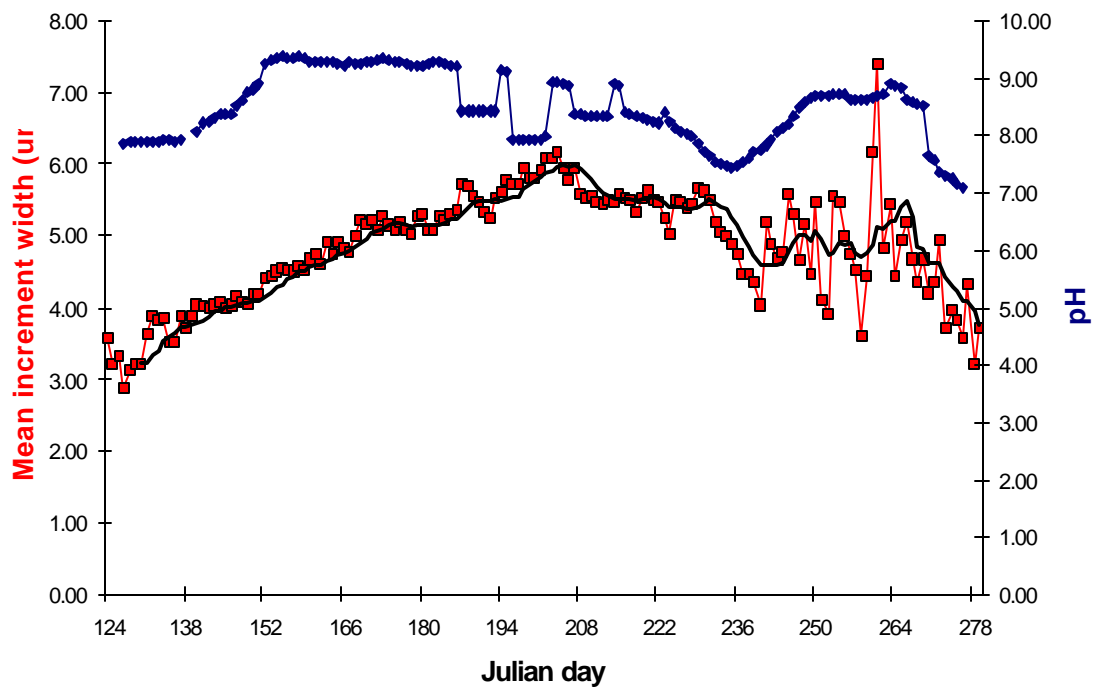
Figure 4. Mean increment width and mean water temperature vs. Julian day. Red dots indicate individual mean increment widths; black line represents seven-day moving average of mean increment widths; blue dots represent seven-day moving average of mean water temperature.
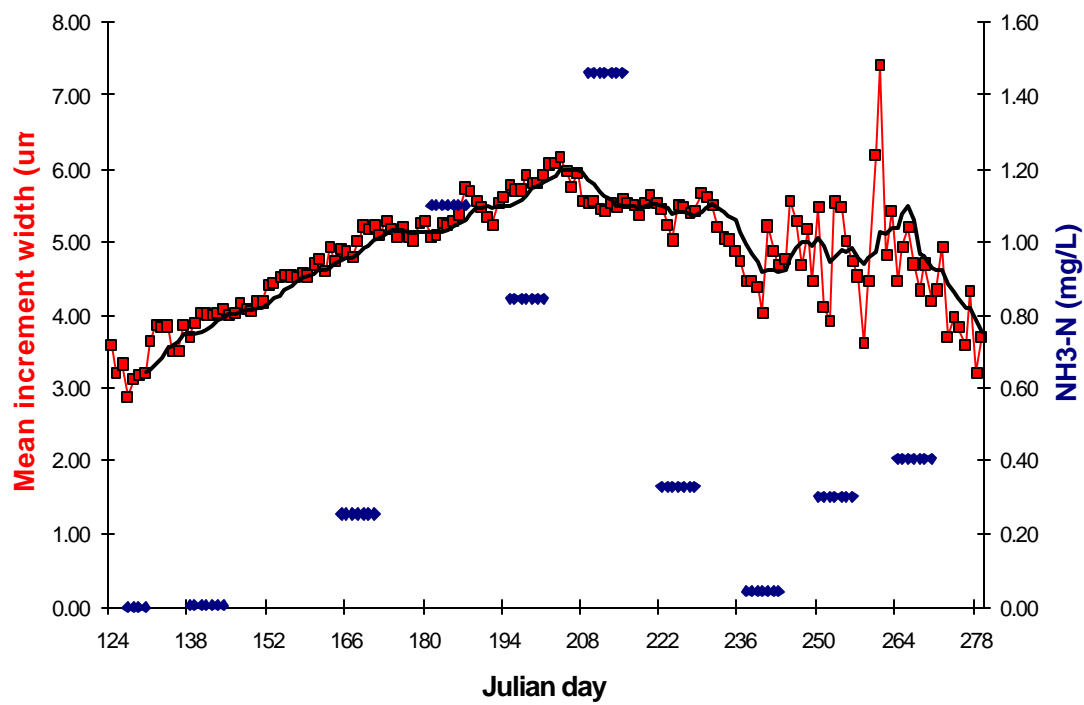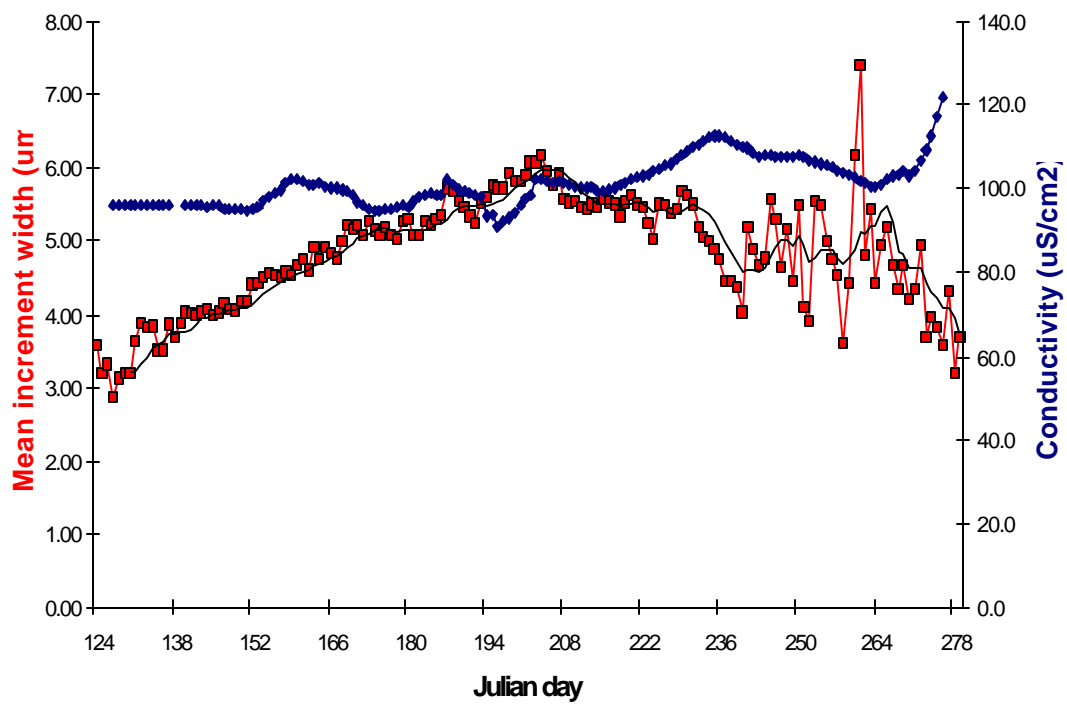
Figure 5. Mean increment width and mean un-ionized ammonia concentration vs. Julian day. Red dots indicate individual mean increment widths; black line represents seven-day moving average of mean increment widths; blue dots represent seven-day moving average of mean un-ionized ammonia concentration.
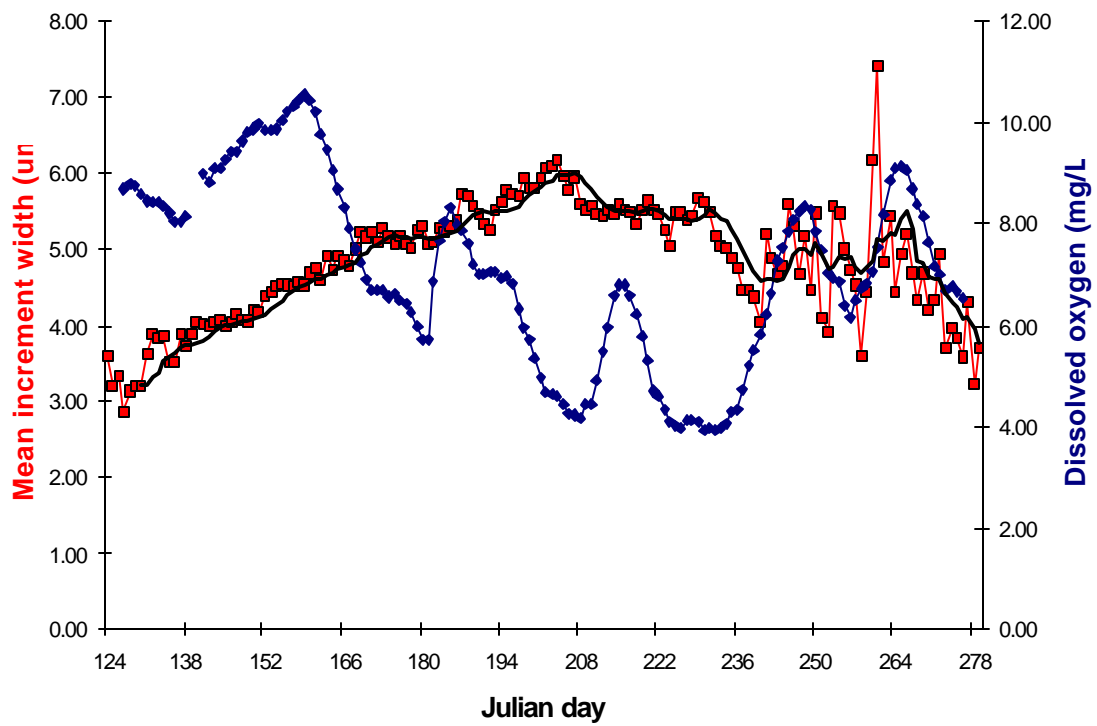
Figure 6. Mean increment width and mean pH vs. Julian day. Red dots indicate individual mean increment widths; black line represents seven-day moving average of mean increment widths; blue dots represent seven-day moving average of mean pH.

Figure 7. Mean increment width and mean conductivity vs. Julian day. Red dots indicate individual mean increment widths; black line represents seven-day moving average of mean increment widths; blue dots represent seven-day moving average of mean conductivity.

Figure 8. Mean increment width and mean dissolved oxygen concentration vs. Julian day. Red dots indicate individual mean increment widths; black line represents seven-day moving average of mean increment widths; blue dots represent seven-day moving average of mean dissolved oxygen concentration.
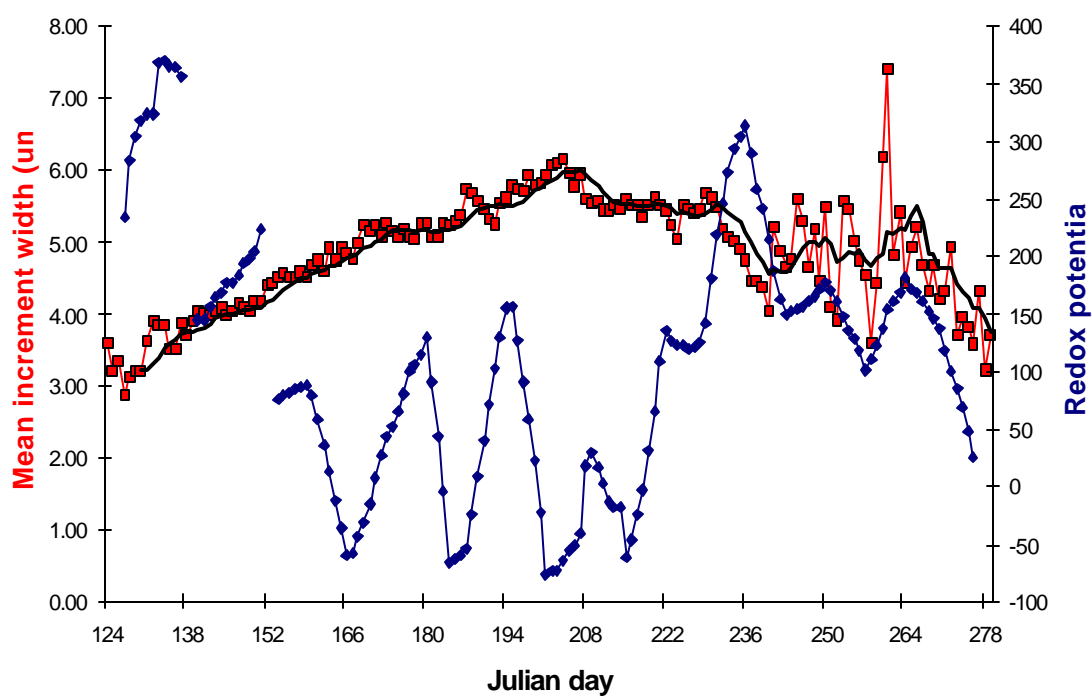
Figure 9. Mean increment width and mean redox potential vs. Julian day. Red
dots indicate individual mean increment widths; black line represents seven-day
moving average of mean increment widths; blue dots represent seven-day
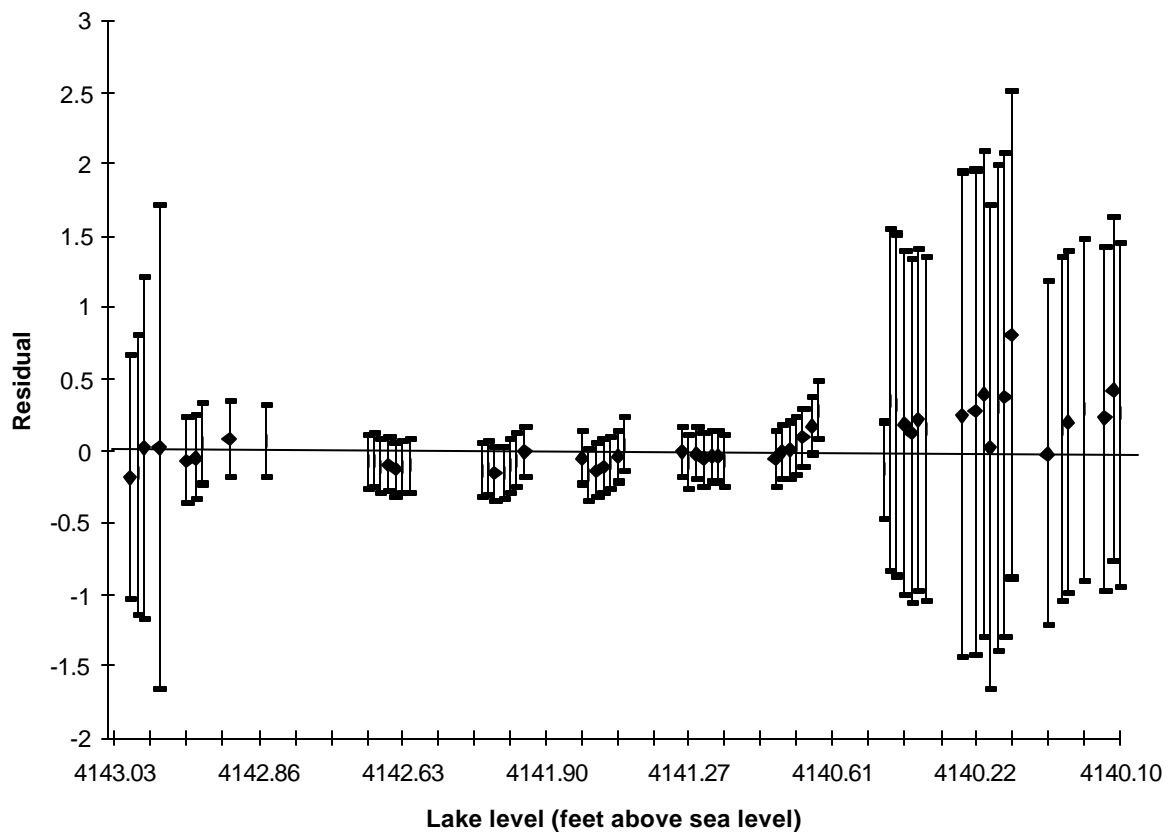moving average of mean redox potential.

Figure 10. Plot of residuals vs. lake level. Residuals were calculated using the linear mixed-effects model containing all water quality parameters as predictors. Black diamonds represent mean residuals; vertical lines represent 95% confidence intervals.
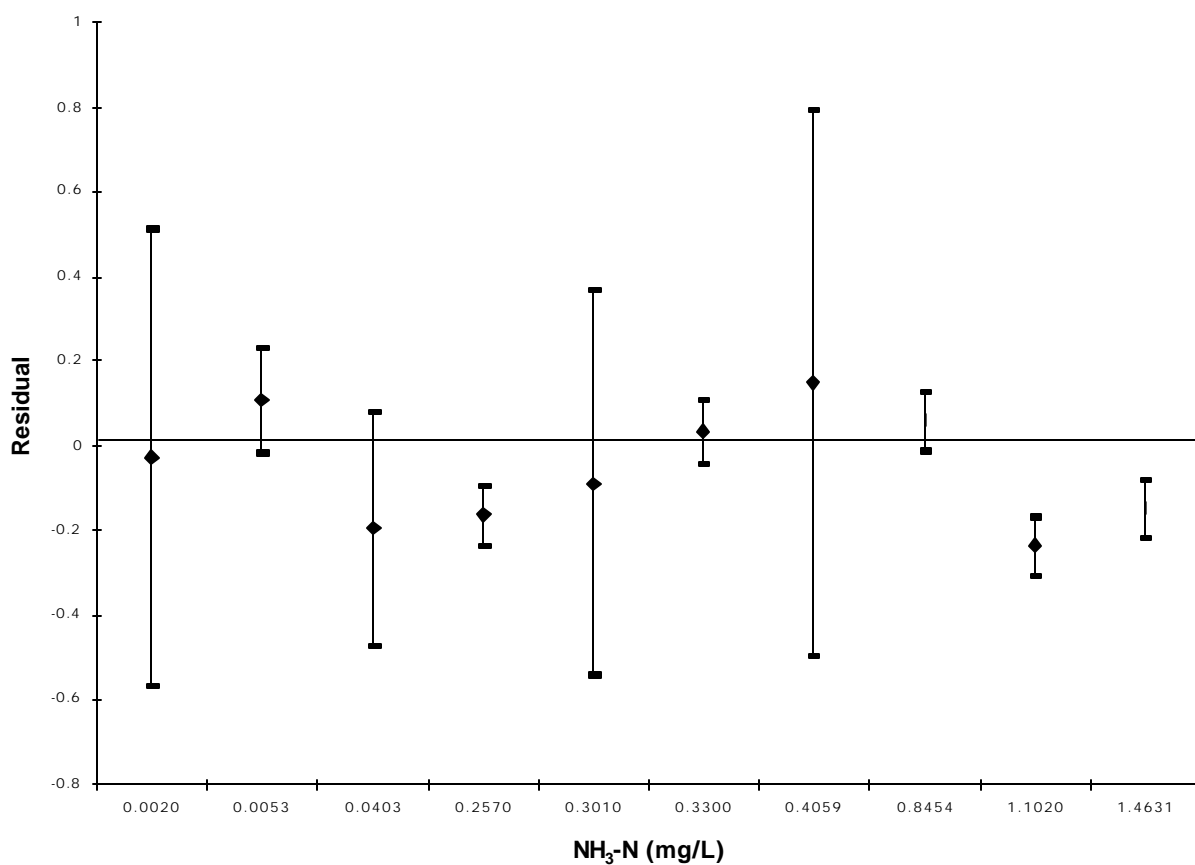
Figure 11. Plot of residuals vs. un-ionized ammonia concentration. Residuals were calculated using the linear mixed-effect model without using un-ionized ammonia as a predictor. Black diamonds represent mean residuals; vertical lines represent 95% confidence intervals.